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19990202 057

Report No. 95-1

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Research report

Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness

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Accepted 28 September 1995

Abstract

During drowsiness, human performance in responding to above-threshold auditory targets tends to vary irregularly over periods of 4 min and longer. These performance fluctuations are accompanied by distinct changes in the frequency spectrum of the electroencephalogram (EEG) on three time scales: (1) during minute-scale and longer periods of intermittent responding, mean activity levels in the (<4 Hz) delta and (4–6 Hz) theta bands, and at the sleep spindle frequency (14 Hz) are higher than during alert performance. (2) In most subjects, 4–6 Hz theta EEG activity begins to increase, and gamma band activity above 35 Hz begins to decrease, about 10 s before presentations of undetected targets, while before detected targets, 4–6 Hz amplitude decreases and gamma band amplitude increases. Both these amplitude differences last 15–20 s and occur in parallel with event-related cycles in target detection probability. In the same periods, alpha and sleep-spindle frequency amplitudes also show prominent 15–20 s cycles, but these are not phase locked to performance cycles. (3) A second or longer after undetected targets, amplitude at intermediate (10–25 Hz) frequencies decreases briefly, while detected targets are followed by a transient amplitude increase in the same latency and frequency range.

Keywords: EEG sleep; Auditory perception; Theta; Gamma; Spindle; ERP

1. Introduction

Human subjects' ability to sustain their initial level of performance during continuous auditory or visual monitoring tasks is limited. After only a few minutes on task, particularly in low-arousal environments, performance of subjects in auditory or visual monitoring tasks often includes periods of intermittent failures to respond to above-threshold targets, alternating with periods of consistent responding. Cycles of relatively good and poor performance tend to last 4 min or longer [4,19] and are experienced by subjects as alternating waves of drowsiness and alertness [24]. Under sustained low-arousal conditions or when subjects are fatigued, these drowsy periods may progress into sleep episodes. Minute-scale changes in the probability of detection of above-threshold signals during

auditory vigilance tasks are accompanied by simultaneous shifts in spectral amplitude of several relatively narrow EEG frequency bands [19], these changes appearing to index the action of brain mechanisms involved in modulating arousal and/or auditory information processing in and near to sleep [27].

One hallmark of the transition from drowsiness to sleep is the appearance of EEG sleep spindles, intermittent oscillatory thalamocortical bursts near 14 Hz [7,26]. Some early EEG studies of drowsiness also associated lapses in auditory detection with increased EEG amplitude in the theta range (4–7 Hz) [2,6,24]. In this study, we explore whether lapses in auditory detection during periods of intermittent detection performance are accompanied by changes in the amplitude of spontaneous EEG activity, and, in particular, whether individual failures to detect auditory target stimuli are more closely associated with increased activity at the sleep spindling frequency or with theta bursts. Finally, we report that different transient perturbations in the EEG spectrum follow presentation of detected and undetected auditory targets and non-target tones.

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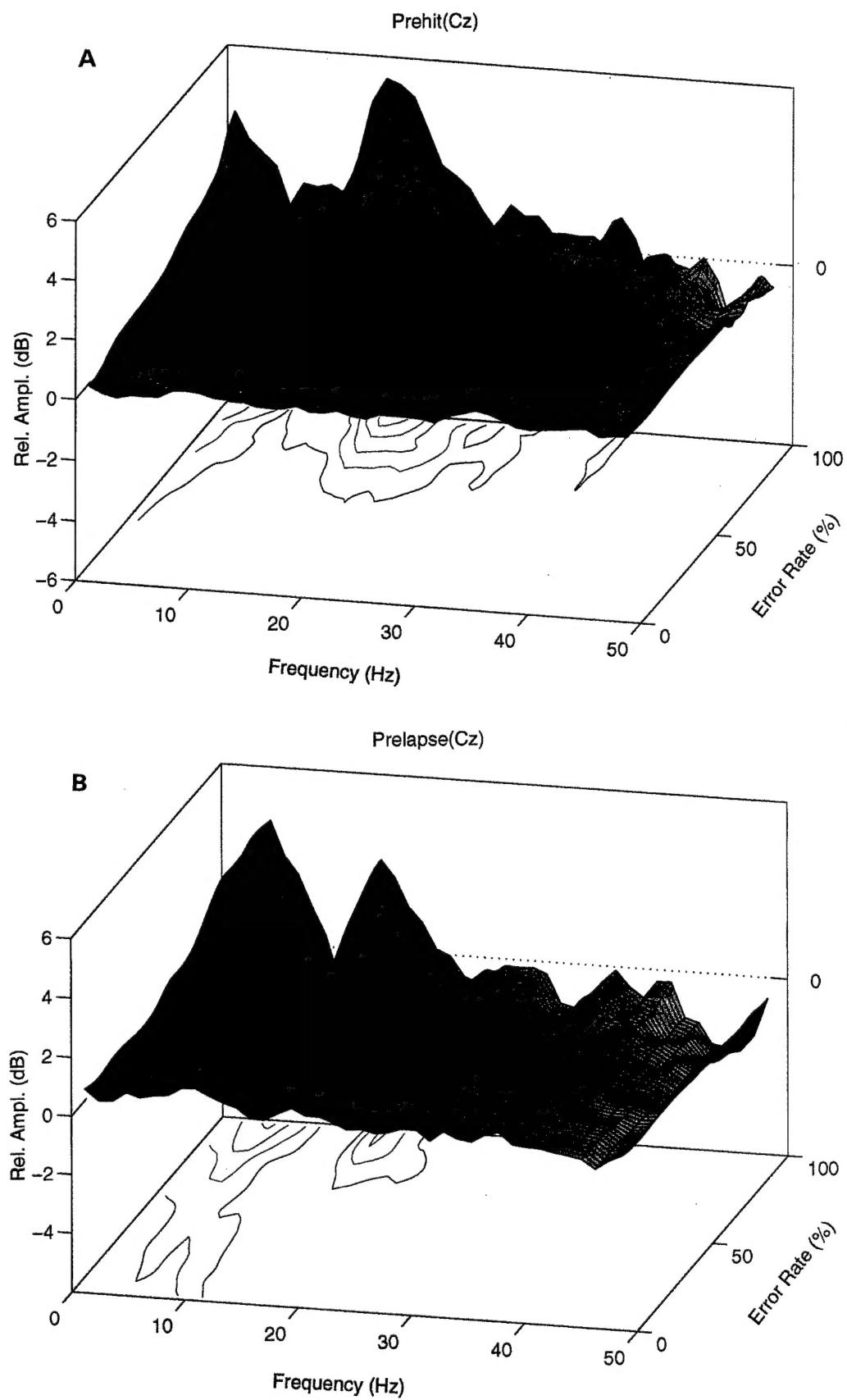


Fig. 1 A,B

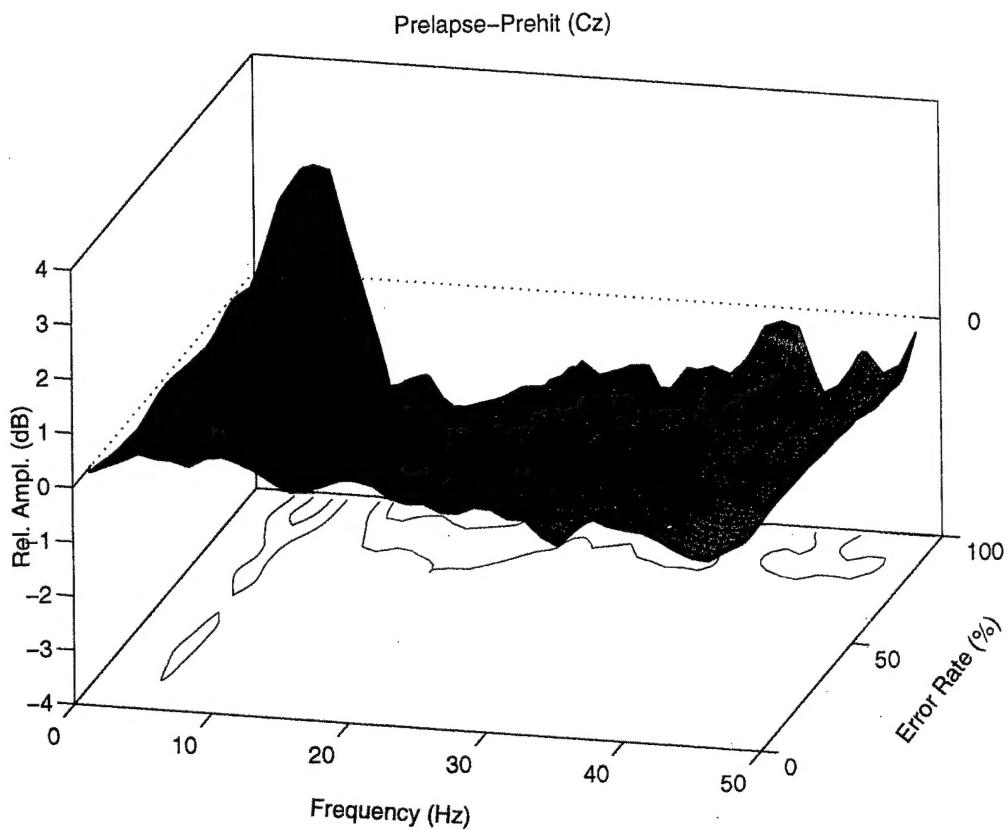


Fig. 1C

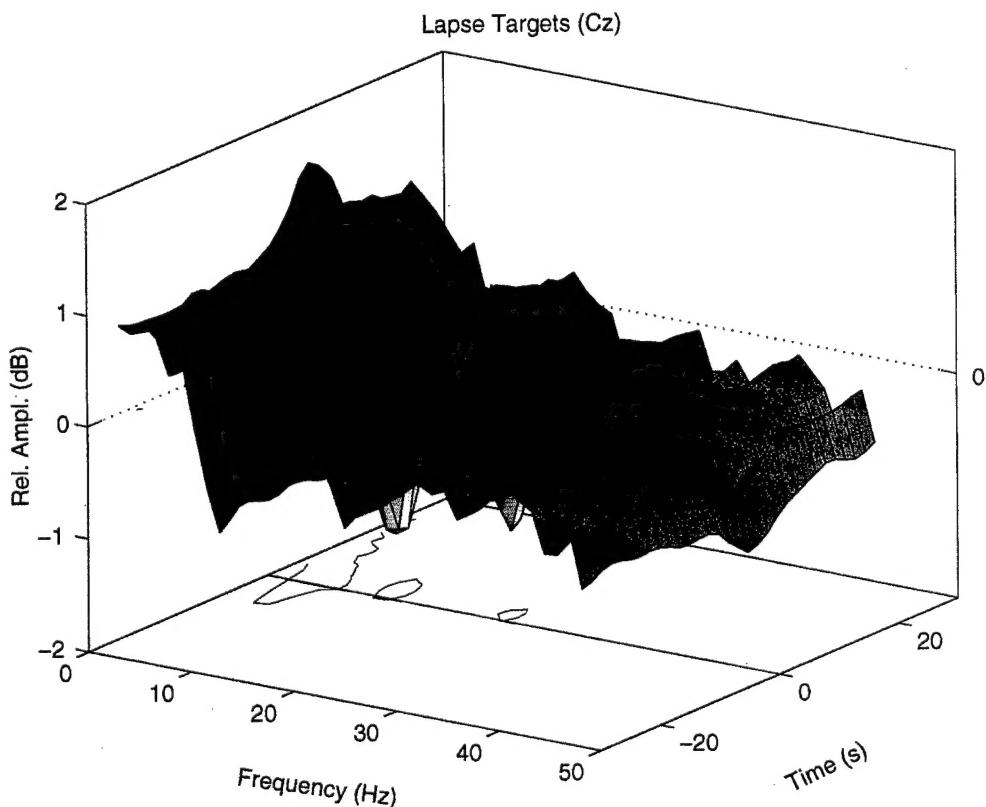


Fig. 2A

2. Materials and methods

Concurrent EEG and behavioral data were collected for the purpose of developing an objective method of monitoring the alertness of operators of complex systems [13,17,19]. Fifteen young adult volunteers participated in five 0.5-h sessions each, during which they pushed one button whenever they detected an above-threshold auditory target stimulus (a brief increase in the level of continuous background noise), and another button whenever they detected a visual pattern on a computer screen in front of them (a slowly-descending line of dots in visual noise).

2.1. Stimuli

Auditory targets consisted of 300 ms increases in the intensity of a 62 dB white noise background (150 ms rise, 110 ms fall), presented 6 dB above their threshold of detectability at pseudorandom time intervals producing a mean rate of 10/min. Brief (50 ms) non-target probe tones of two frequencies (20% 568 Hz, 80% 1098 Hz) were interspersed between the target noise bursts at 2–4 s intervals. Visual targets were vertical lines of dots presented in a slowly descending (2 lines/s) visual noise ‘waterfall’ pattern at a mean rate of 1/min. Sessions were conducted in a small, warm, and dimly-lit experimental chamber. Visual task data will be reported elsewhere.

2.2. Data collection

EEG was collected from two electrodes at the vertex and posterior midline (Cz and Pz/Oz, midway between Pz and Oz), referred to the right mastoid, at a sampling rate of 312.5 Hz after analogue filtering (Grass Model 12, bandpass 0.1–100 Hz, 12 dB/octave). Channel locations were selected as likely to contain independent alertness information on the basis of previous studies [19]. Bipolar vertical and horizontal electrooculogram (EOG) data were also

recorded for use in artifact rejection. Data windows containing potential deviations from baseline of more than 75 μ V were rejected from analysis. Three sessions each from ten subjects containing sufficient (mean \pm S.D., 56 \pm 26) response lapses were used in the analysis.

2.3. Local error rate

A time-varying, causal behavioral index of alertness, local error rate, was defined by computing a moving average probability of detection of auditory targets smoothed using a 95-s wide exponential moving window (90% down 95 s back) whose width and shape were chosen to increase smoothness of the resulting measure while decreasing the (23 s) time lag from the leading edge of the window to its center of gravity. Time-varying EEG spectra with 0.6 Hz resolution were computed at 1.64-s intervals using running median averages of FFT transforms of Hanning-windowed 0.82-s data epochs with 50% overlap (zero-padded to 512 points/1.64 s). The median filtering window spanned seven overlapping 0.82-s data windows, encompassing 3.28 s of data. The four median-filtered spectral estimates in each 1.64-s interval were then averaged.

2.4. Error-sorted spectra

Changes in the EEG spectrum as a function of error rate were computed by separately averaging log spectra in 4-s epochs preceding detected (hit) and undetected (lapse) target presentations, sorting these spectra according to the prevailing error rate, and then smoothing the results using a Hanning window (encompassing a 30% error-rate range) which was moved through the error-sorted data in 5% error-rate steps. The mean log spectrum during the first 2 min of error-free performance was then subtracted from each spectral trace, yielding hit- and lapse-related error-sorted spectra revealing mean changes in the EEG spec-

Fig. 1. Grand mean error-sorted spectra at the vertex (Cz). Mean EEG log spectra during 4 s intervals preceding target presentations were sorted by local error rate (see text) and normalized by subtracting the mean log spectrum of the first 2 min of alert zero-error performance in each session. Grand means of data from 3 sessions for each of 10 subjects. Contour level intervals: 1 dB. (A) Error-sorted spectrum for periods preceding detected targets (hits) shows error rate-related increases in low-frequency (< 4 Hz) and near-14 Hz activity. (B) Error-sorted spectrum preceding undetected targets (lapses) has another peak near 5 Hz. (C) Difference between (A) and (B) (prelapse – prehit) showing, during high error-rate periods, a relative increase in near 5-Hz activity before lapses, accompanied by a relative decrease at higher frequencies.

Fig. 2. Event-related spectral perturbation (ERSP) transforms at Cz of 56-s epochs centered on targets presented when local error rate was between 20% and 80%. Vertical scale is log amplitude (in dB) relative to baseline. Grand means of 30 sessions from 10 subjects. Contour levels: in (A), \pm 1 dB; in (B–D), \pm 4 and 8 S.D. (in the first 8 s of the plotted ERSP epoch). (A) Alert-normalized ERSP time locked to undetected targets (lapses). Note the phasic EEG amplitude increase near 5 Hz superimposed on tonically increased (1–6 Hz) slow activity. (B) Single-trial baseline normalized ERSP transform of the lapse-related data (see text). Note the prestimulus increase near 5 Hz and (less noticeable) decrease near 40 Hz, and the brief suppression of activity at intermediate frequencies after the stimulus. (C) Single-trial normalized ERSP for epochs surrounding detected targets (hits). Note the anticipatory relative decrease in amplitude near 5 Hz, the simultaneous increase above 30 Hz, and the stimulus-induced ridge of increased 10–20 + Hz activity. (D) Single-trial normalized (lapse-hit) difference between (B) and (C), containing features common to both transforms. (E) Plot of the time course of *F*-statistics for lapse-related and hit-related ERSP log amplitude differences in three EEG frequency bands. The dashed line shows the ($P = 0.001$) significance threshold for independent comparisons. Consistent group differences in 4–6 Hz and 35–50 Hz band amplitudes begin near 10 s before lapses, whereas at 10–11 Hz, an amplitude difference appears only after stimulus onset.

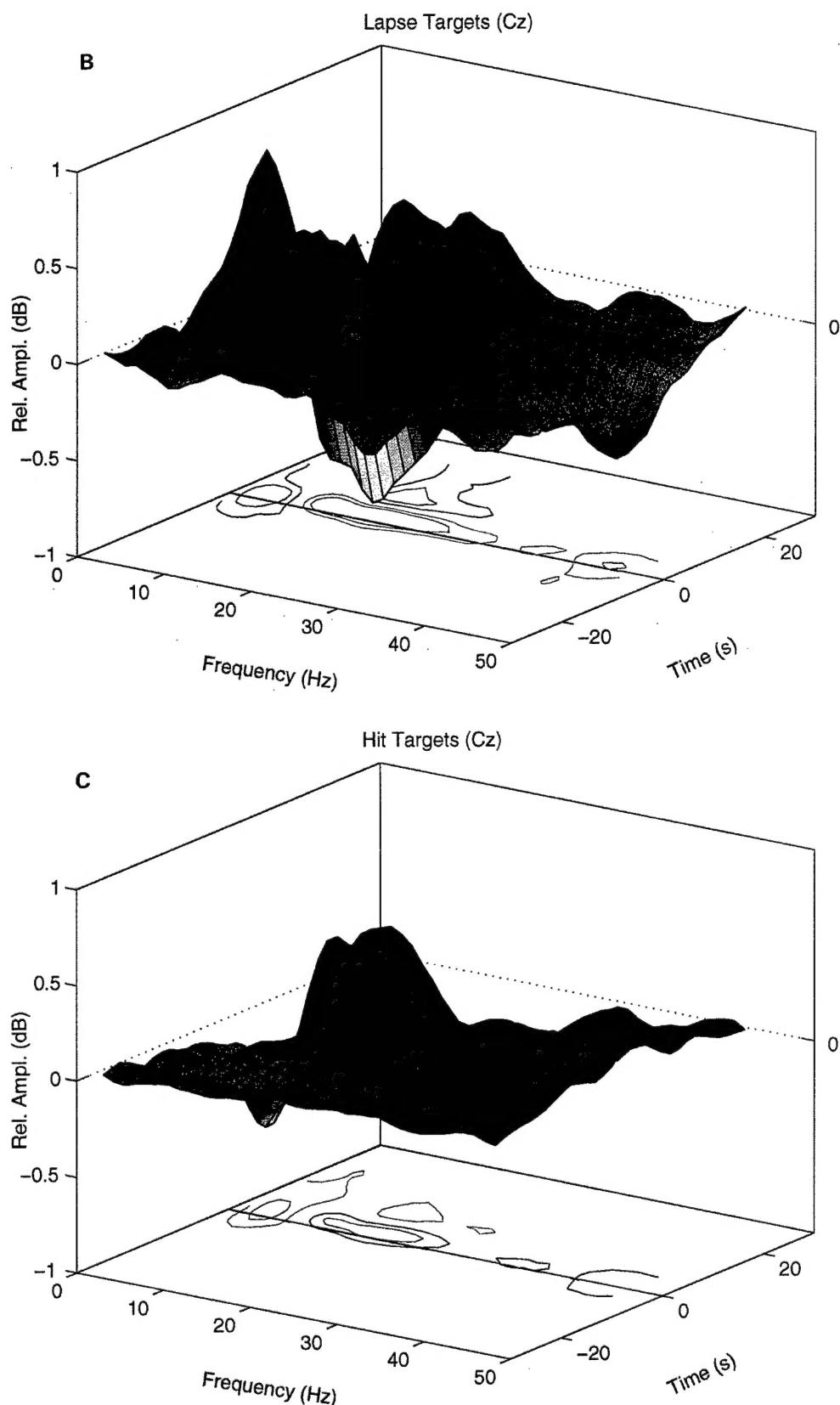


Fig. 2. (continued).

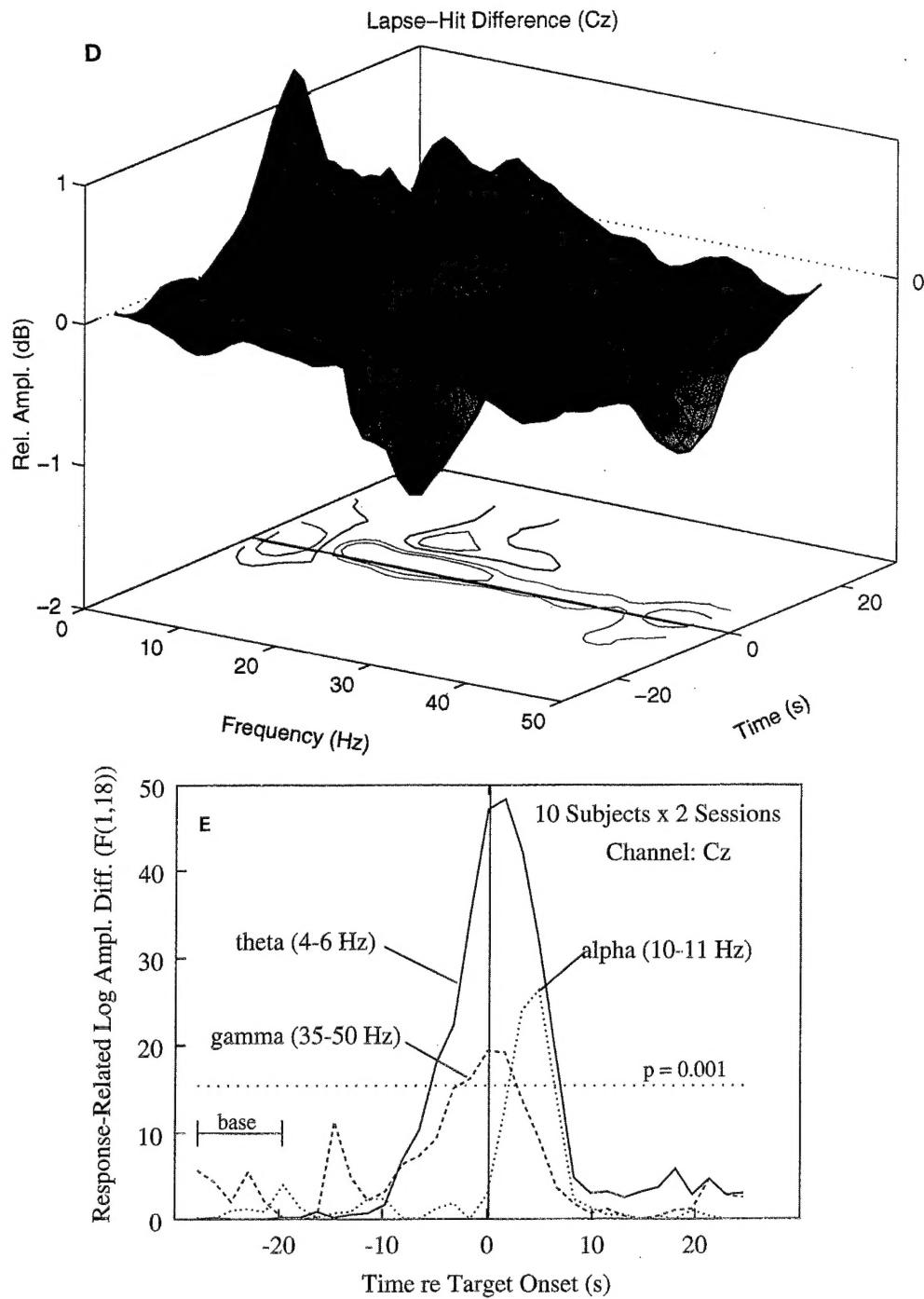


Fig. 2. (continued).

trum accompanying different levels of performance (see Fig. 1).

2.5. Spectral perturbations

The time course of event-related changes in the amplitude of oscillatory EEG activity time locked, but not necessarily phase locked, to experimental events can be measured using normalized time-frequency transforms,

previously called event-related spectral perturbations (ERSPs) [16]. Averages of time-frequency transforms of EEG epochs time locked to experimental events can measure event-related modulations of EEG amplitude at a wide range of frequencies and time scales (tenths of seconds [12] to minutes or longer [9,19]). Time- and frequency-specific ERSP features are largely independent of concurrent features of time-domain response averages (event-related potentials or ERPs). ERPs contain potential devia-

tions occurring at fixed times and in fixed phases relative to experimental events, while ERSPs record changes in the amplitude of EEG oscillations irrespective of their phase at event onsets. Here, ERSPs time locked to hit and lapse target noise bursts, and to non-target tones, were computed by averaging logarithmic time-frequency amplitude transforms of 54-s spectral epochs surrounding stimulus onsets. Two types of normalization were applied (see Fig. 2).

3. Results

3.1. Error-sorted spectra

During periods of poor detection performance, the mean error-sorted EEG spectrum at the vertex prior to lapses (Fig. 1A) contains two prominent maxima – relative increases in EEG amplitude near 5 Hz and 14 Hz, plus a smaller increase at frequencies below 5 Hz. At high error rates, mean amplitude near 10 Hz at site Pz/Oz also decreased in most subjects below its eyes-open baseline level. The 14-Hz peak appears only when error rate is above 80%, consistent with the emergence of 14-Hz spindles at sleep onset [7]. At high error rates, the error-sorted spectrum at Cz prior to hits (Fig. 1B) also contains a peak near 14 Hz, but has no peak near 5 Hz. During high error-rate periods, 14-Hz amplitude is nearly equally as elevated before lapses as before hits, while in our 10 subjects mean amplitude near 5 Hz is significantly larger before lapses at all non-zero error rate levels ($F_{1,9} > 22.9$, $P < 0.001$). The (lapse minus hit) difference between the two error-sorted spectra (Fig. 1C), therefore, contains a circa 5-Hz positivity at all error rates accompanied, at high error rates, by a general decrease in activity above 8 Hz – but no feature at 14 Hz.

3.2. Spectral perturbations

Fig. 2A shows the mean changes in the EEG log spectrum at Cz before, during, and after undetected noise burst targets (lapses) presented during periods of intermittent (20–80% error rate) detection performance in the same 30 sessions. Single-session ERSPs were normalized by subtracting the mean log spectrum during the first two minutes of error-free performance, to show both the tonic EEG spectral changes associated with periods of non-zero (20–80%) error rate, and phasic EEG changes associated with detection lapses during these periods. The figure shows the expected tonic amplitude increase at 5 Hz and below, and also a phasic increase near 5 Hz beginning several seconds before delivery of undetected targets.

To study this and other features of Fig. 2A in more detail, time-frequency transforms of data epochs time locked to undetected (lapse) target presentations were individually normalized by subtracting a pre-stimulus baseline log spectral estimate from each spectral trace. The baseline

estimate was the mean log spectrum in an exponential window with leading edge 10 s before, and its (90%-down) trailing edge 105 s before target onset. The resulting normalized transforms, containing time-varying spectral fluctuations relative to the mean spectrum in the preceding 105-s period, were then averaged and their grand mean across subjects and sessions was calculated. (Note that baseline periods included an average of 17 previous target and 34 non-target tone presentations.) Target hit-related ERSP averages were computed by the same procedure.

Lapse-related (Fig. 2B) and hit-related (Fig. 2C) ERSPs differ significantly in three ways: (1) the mean increase (or decrease) in 5-Hz activity surrounding target presentation; (2) the opposing amplitude decrease (or increase) above 35 Hz; (3) the trough (or ridge) amplitude perturbation at 10–25 Hz appearing after hit (or lapse) target presentations, respectively, with a frequency extremum at 11 Hz. As the hit and lapse target ERSPs in Fig. 2B,C are negatively correlated ($r = -0.89$), their difference (Fig. 2D) emphasizes their common features.

Fig. 2E shows the time course of $F_{1,18}$ -statistics for hit/lapse differences at each time point in 20 sessions (two sessions containing the most lapses from each of the 10 subjects). The figure shows the time course of this statistic for response-related log amplitude differences in theta, alpha, and gamma frequency bands. Whereas differences in theta and gamma band activity begin nearly 10 s before the stimulus, a response-related difference in alpha band amplitudes appears only after stimulus onset.

3.3. Performance cycles

Next, we asked whether the phasic increases in 5-Hz activity before and after lapses were accompanied by transient changes in target detection probability. As might be expected, the probability of subjects of detecting targets presented immediately before and after detected and undetected targets, respectively, differed from one another and from the local error-rate baseline. Surprisingly, both these performance-related differences had similar and well-defined time courses, which were quantified as the probability of a lapse in a 1.64-s time window moved through the 58-s ERSP epoch in 0.41-s steps. Fig. 3A shows results at site Pz/Oz; results at Cz were similar. In this and following figures showing event-related error rate trends, the steepness and width of the error rate extrema at time zero reflect the 1.64-s smoothing width used and the minimum 1-s interval between target presentations.

Different sessions from the same subject gave highly similar error-rate perturbations (Fig. 4A) which closely paralleled the time course of the 4–6 Hz EEG amplitude trends in group and most single subject data (Fig. 3B,C and Fig. 4B). Ten seconds after hits, both error rate and 4–6 Hz amplitude settled at somewhat lower levels than their pre-stimulus baselines, presumably reflecting a net arousing effect of target detections and/or responses. Fig.

4A shows differences between the time course of error rate changes time locked to lapses and hits, respectively. The top trace shows the grand mean error-rate difference; the traces below it are for 20 single sessions, with pairs of sessions from the same subject superimposed. Fig. 4B

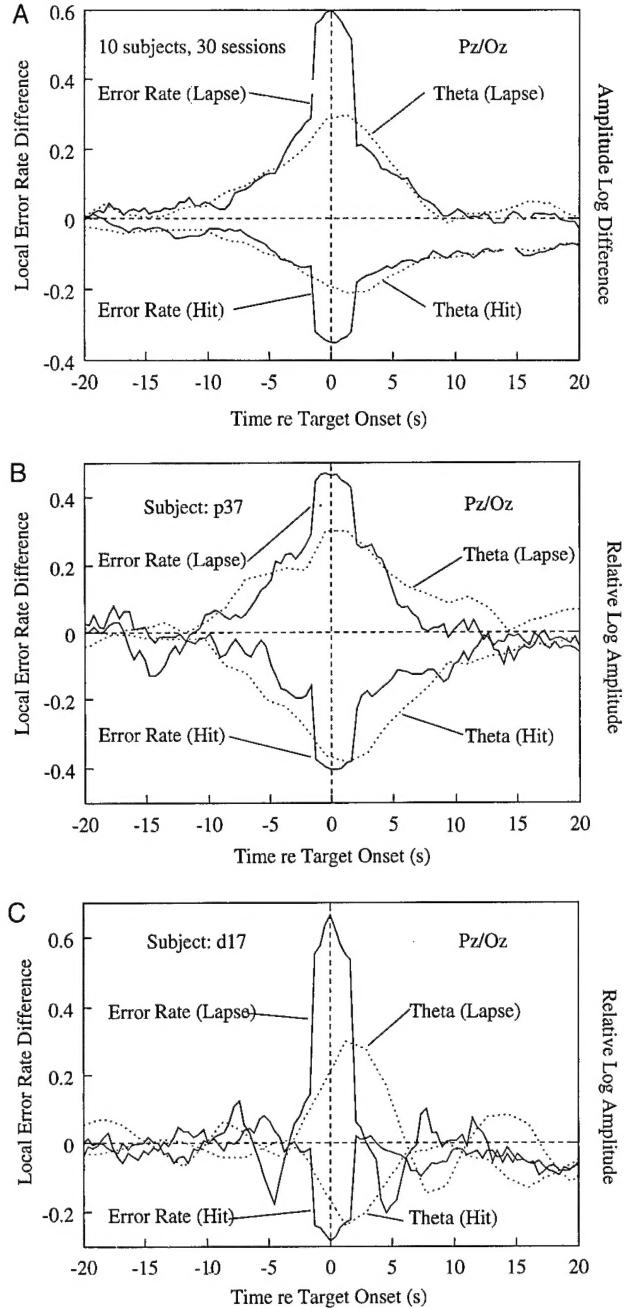


Fig. 3. Time course of event-related error rate and relative 4–6 Hz EEG log amplitude at Pz/Oz (each smoothed in a 1.64-s moving window) before and after the same detected (hit) and undetected (lapse) targets as in Fig. 2A. (A) Grand means for 30 sessions from 10 subjects. Note divergence of all four measures from 10 s before to 10 s after target presentations. (B) Time course of relative 4–6 Hz log amplitude and error rate in one of the seven subjects showing the error-rate trend seen in the grand mean (Fig. 3A). (C) Same for one of three subjects not showing 15–20 s EEG and error-rate cycles (see Fig. 4A).

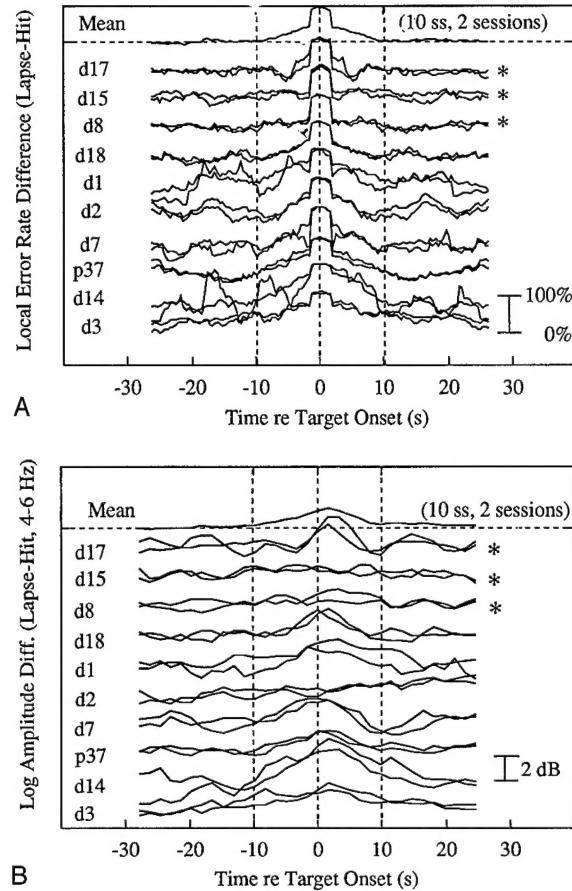


Fig. 4. Time course of differences in response-related (A) error-rate and (B) 4–6 Hz amplitude time series for site Pz/Oz. Differences between lapse and hit event-related records (like those shown in Fig. 3) are shown smoothed with a 1.64-s moving window. Top traces: grand means. Lower traces: individual sessions, with pairs of sessions from the same subject superimposed. Subjects data are arranged in the same order in both panels, with data from the three subjects showing no evidence of 15–20 s performance cycles marked with asterisks. Subject codes are listed on the left of each panel.

shows the time course of 4–6 Hz amplitude differences in the same sessions. Note the strong within-subject replicability of both the performance and amplitude cycles, and the stable between-subject differences. The top three trace pairs in each panel are from three subjects who do not show response-related 15–20 s performance cycles. The 4–6 Hz theta amplitude trends for at least two of these three subjects (Fig. 4B, top two pairs) likewise contain no 15–20 s cycles.

4. Discussion

Our results show that variations in sustained auditory detection performance have distinct EEG spectral correlates on three time-scales, here categorized as tonic changes, phasic cycles, and transient perturbations.

4.1. Tonic changes

During minute-scale and longer periods of intermittent responding, mean EEG amplitudes in the delta (< 4 Hz), theta (4–6 Hz), and sleep-spindle (near 14 Hz) bands tend to increase at Cz and at Oz/Pz. During these periods, delta and 14-Hz amplitudes are equally as large before hits as before lapses, while 4–6 Hz activity is significantly larger before lapses than before hits.

During sleep, behavioral and brain responsiveness to sounds is decreased, and communication of afferent auditory information between the thalamus and auditory cortex is restricted or gated [26,27]. Although a tonic increase in activity at the human sleep spindle frequency (near 14 Hz) [7] accompanies sustained decrements in detection probability, 14-Hz amplitude is not related to the detection of individual targets (Fig. 1C). Our analyses do not determine what portion of the 14-Hz peaks in Fig. 1A,B reflects the appearance of classic sleep spindles. However, the lack of a 14-Hz feature in Fig. 1C strongly suggests that sleep spindles, hallmarks of transition to slow-wave sleep, cannot be directly involved in intermittent gating of sensory information during drowsiness, although they may have a role in producing tonic changes in auditory sensitivity during sleep onset [26].

The most important conclusion to be drawn from the error-sorted spectra (Fig. 1) is that during periods of intermittent performance, individual detection lapses are associated with increased activity near 5 Hz, not with 14-Hz sleep spindles or increased delta activity. ERSP (Fig. 2) and event-related error-rate (Fig. 3) analyses demonstrate that the observed 4–6 Hz differences arise from phase-locking of 15–20 s EEG and performance cycles.

4.2. Phasic cycles

During periods of inconsistent responding, seven of our ten subjects show 15–20 s cycles in detection probability, closely paralleled by opposing changes in EEG amplitudes near 5 Hz and above 35 Hz. In accord with claims of some early EEG studies, undetected targets are preceded by increased activity near 5 Hz, while EEG activity above 35 Hz tends to increase prior to detected targets.

Second-order spectral analyses of amplitude variance at each EEG frequency (not shown), applied to the same epochs used to compute the ERSPs (Fig. 2), revealed a peak cycle length between 15 and 20 s per cycle over a wide range of EEG frequencies, consistent with other reports [20]. The 15–20 s theta and gamma perturbations in Fig. 3A, then, may result from mutual phase locking of spontaneous amplitude fluctuations at these frequencies, uncorrelated with 15–20 s fluctuations at low (< 4 Hz) and intermediate frequencies (10–25 Hz). The fact that the theta-band amplitude cycles are also time locked to performance cycles (Fig. 3A) suggests that in humans intermit-

tent gating of auditory information transmission during drowsiness may be intimately connected to the occurrence 4–6 Hz activity.

While neurophysiological mechanisms underlying auditory gating have been discussed [26,27], and 20 s cycles in EEG amplitude have been found to be synchronized to sleep onsets in rat neocortex [18], the behavioral and physiological distinction we report here between sleep spindling and lapse-related theta activity does not seem to have been observed in animal brains. Note also that we cannot rule out possibilities that some or all lapses in these experiments arose from subjects' sleep-related inability to recall the significance of the tones or to press the response button, although in our own experience as subject (tpj) and pilot subject (sm), all three dimensions of awareness (auditory, situational, and somatic) seemed to covary.

This is not the first report that changes in theta and gamma band EEG amplitudes are linked to changes in attention and awareness [8,11]. Intermittent vigilance decrements similar to the 15–20 s cycles we report here have recently been reported in monkeys performing a continuous visual task, and have been correlated with cyclic decreases in locus coeruleus activity [22]. Conversely, noradrenergic locus coeruleus activation is known to produce behavioral alerting, accompanied by a rapid shift of the cortical EEG spectrum from low to high frequencies [28]. Possibly, a similar modulator may underlie the 15–20 s performance and EEG fluctuations seen both in quietly resting [20] and here in drowsy humans. More than one brain arousal subsystem may also be involved in producing them [26].

Our observed pre-stimulus increase in theta-band EEG prior to lapses in these experiments confirms and further quantifies early reports [6], most notably a 1962 study of Williams et al. [29] in which this phenomenon was seen in EEG tracings of some subjects after 30 h of sleep deprivation. In other early EEG studies, 'low-level irregular' theta activity was associated with self-reports of day-dreaming and 'floating' sensations typical of the hypnagogic period preceding sleep onset [24]. Most recent studies of theta band EEG, however, have focussed on dissimilar phenomena associated with arousal and attention, including rhythmic slow activity (RSA) in the septohippocampal and related system appearing in animals during volitional movements [14] and frontal midline theta EEG in humans associated with mental effort [10].

The increased gamma-band activity preceding detected targets in our data is compatible with hypotheses that transient phase correlations among local gamma band oscillations in the cortex and thalamus may help support allocation of perceptual attention [5,8,15,23]. Although we cannot rule out possible contributions of muscle activity to changes in gamma band activity prior to detected or undetected targets, muscle activity normally contains frequencies below 35 Hz, the lower edge of our performance-related gamma-band difference, suggesting

that the phasic gamma band phenomenon shown in Fig. 2 arises predominately from performance-related changes in brain activity.

4.3. Transient perturbations

Successfully detected auditory targets are followed by a brief increase in 10–25 Hz EEG activity beginning a second or more after stimulus onset, while undetected targets are followed by a brief relative amplitude decrease in the same time and frequency range.

The appearance of 10–25 Hz spectral perturbations following (but not preceding) undetected (Fig. 2B) as well as detected (Fig. 2C) targets implies that the brain system responsible for these EEG modulations also detects lapse targets, to which subjects do not respond. ERSPs (not shown) time locked to onsets of the frequent (16/min) non-target tones in these sessions contained no comparable response feature, implying that the EEG modulator responsible for the 10–25 Hz response can also distinguish target noise bursts from non-target tones, even though the non-target tones in these experiments were perceptually more salient than the relatively faint target noise bursts. Similarly, in auditory experiments reported earlier [16], a ‘ridge’ of augmented 11–19 Hz activity induced by very brief target tone pips was found to be twice as large that induced by intense (84 dB SL), long-lasting (1 s) non-target tones.

Note that this attention-related 10–25 Hz perturbation appears much later than attention-related features of the auditory ERP, such as the P300, but closer in latency to attention-related autonomic responses such as the evoked pupillary response [1]. In general, the magnitudes of ERSP features (0.5–2 dB, 5–25%) in this and previously-reported experiments are comparable in size to task-related differences in local brain metabolism reported in many PET and fMRI brain studies [21,25], suggesting a possible relation between EEG spectral perturbations and the size of local brain blood-flow changes.

4.4. Conclusions

Concurrent activity on a wide range of time scales is a basic fact of brain physiology [3]. Our results show that during periods of impaired performance on an auditory vigilance task, at least three time scales characterize the dynamics of variations in auditory detection performance and the EEG spectrum. Overall, changes in error rate in auditory detection are dominated by irregular waves of performance changes lasting 4 min and longer [4,19]. Within these, phasic 15–20 s cycles in detection performance are phase locked to counterbalanced changes in EEG amplitudes near 5 Hz and above 35 Hz, respectively. Finally, auditory stimuli induce transient and variable perturbations in the EEG amplitude spectrum which can be observed by averaging normalized time-frequency trans-

forms (ERSPs) of event-related data epochs. In particular, faint target noise bursts (but not more salient non-target tones) in our experiments induce transient time locked perturbations in mean EEG amplitudes at intermediate frequencies (10–25 Hz), whose sign (positive or negative) depends on whether or not the subject responds to the target.

Further understanding of characteristic time and frequency scales involved in cognitive brain processing during sleep and waking may lead to a deeper appreciation of the organization of human consciousness and performance, and may also have practical applications in monitoring the alertness of operators of complex systems [13,17].

Acknowledgements

The authors acknowledge the valuable contributions of F. Scot Elliott and Mark Postal in collecting and archiving the data, and thank Mark Inlow and two anonymous reviewers for helpful suggestions, and Terry Sejnowski for technical support. This work was supported by the Department of the Navy, Naval Medical Research and Development Command, Bethesda, Maryland under work unit ONR.WR.30020(6429). The views expressed in this article are those of the authors and do not reflect the official policy or position of the Department of the Navy, Department of Defense, nor the U.S. Government. Approved for release, distribution unlimited.

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REPORT DOCUMENTATION PAGE

Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing the collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden, to Washington Headquarters Services, Directorate for Information Operations and Reports, 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302, and to the Office of Management and Budget, Paperwork Reduction Project (0704-0188), Washington, DC 20503

1. AGENCY USE ONLY (Leave blank)	2. REPORT DATE April 95	3. REPORT TYPE & DATE OVERDUE Interim 1995
4. TITLE AND SUBTITLE Tonic, phasic, and transient EEG correlates of auditory awareness in drowsiness		5. FUNDING NUMBERS Program Element: Work Unit Number: ONR Reimbursable-6429
6. AUTHOR(S) Scott Makeig & Tzzy-Ping Jung		
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Naval Health Research Center P.O. Box 85122 San Diego, CA 92186-5122		8. PERFORMING ORGANIZATION Report No. 95-1
9. SPONSORING/MONITORING AGENCY NAMES(S) AND ADDRESS(ES) Naval Medical Research & Development Command National Naval Medical Center 8901 Wisconsin Ave Bldg 1 T2 Bethesda, MD 20889-5606		10. SPONSORING/MONITORING AGENCY REPORT NUMBER
11. SUPPLEMENTARY NOTES Published in <u>Cognitive Brain Research</u> , 1996, 4, 15-25		
12a. DISTRIBUTION/AVAILABILITY STATEMENT Approved for public release; distribution is unlimited.		12b. DISTRIBUTION CODE A
13. ABSTRACT (Maximum 200 words) During drowsiness, human performance in responding to above-threshold auditory targets tends to vary irregularly over periods of 4 min and longer. These performance fluctuations are accompanied by distinct changes in the frequency spectrum of the electroencephalogram (EEG) on three time scales: (1) during minute-scale and longer periods of intermittent responding, mean activity levels in the (<4 Hz) delta and (4-6 Hz) theta bands, and at the sleep spindle frequency (14 Hz) are higher than during alert performance. (2) In most subjects, 4-6 Hz theta EEG activity begins to increase, and gamma band activity above 35 Hz begins to decrease, about 10 s before presentations of undetected targets, while before detected targets, 4-6 Hz amplitude decreases and gamma band amplitude increases. Both these amplitude differences last 15-20 s and occur in parallel with event-related cycles in target detection probability. In the same periods, alpha and sleep-spindle frequency amplitudes also show prominent 15-20 s cycles, but these are not phase locked to performance cycles. (3) A second or longer after undetected targets, amplitude at intermediate (10-25 Hz) frequencies decreases briefly, while detected targets are followed by a transient amplitude increase in the same latency and frequency range.		
14. SUBJECT TERMS EEG Sleep Auditory perceptions		15. NUMBER OF PAGES 11
		16. PRICE CODE
17. SECURITY CLASSIFICATION OF REPORT Unclassified	18. SECURITY CLASSIFICATION OF THIS PAGE Unclassified	19. SECURITY CLASSIFICATION OF ABSTRACT Unclassified
		20. LIMITATION OF ABSTRACT Unclassified